



Spatial Ecology of Wolverines at the Southern Periphery of Distribution

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ABSTRACT Wolverines (*Gulo gulo*) in the conterminous United States have experienced range contraction, are uncommon, and have been designated as warranted for protection under the United States Endangered Species Act. Data from the southern edge of the wolverine's circumpolar distribution is sparse, and development of effective conservation strategies would benefit from a more complete understanding of the species' ecology. We captured and radio-monitored 30 wolverines in the Greater Yellowstone Ecosystem (GYE), tested for seasonal habitat selection by elevation band, and examined a suite of spatial characteristics to clarify our understanding of the wolverine's niche. Wolverines in GYE selected for areas >2,600 m latitude-adjusted elevation (LAE; $n = 2,257$ wolverine locations [12 F, 6 M]). Wolverines avoided areas <2,150 m LAE, including during winter when the vast majority of ungulates are pushed to these elevations by deep snow. Wolverine home ranges were large relative to body size, averaging 303 km² for adult females and 797 km² for adult males ($n = 13$ [8 F, 5 M] and 33 wolverine-years). Resident adults fit with Global Positioning System (GPS) collars used an area >75% the size of their multi-year home range in an average of 32 days ($n = 7$ [5 F, 2 M]). Average movement rates of 1.3 km/2-hr indicated that both sexes move distances equivalent to the diameter of their home range every 2 days or the circumference of their home range in <1 week ($n = 1,329$ 2-hr movements, $n = 12$ individuals [7 F, 5 M]). This capability for movement, the short time-frame over which home ranges were developed, and a lack of home range overlap by same sex adults ($\bar{x} = 2.1\%$ overlap, 90% CI = 0.0–4.8%, $n = 22$ pairs) suggested territoriality. We estimated wolverine density to be 3.5/1,000 km² of area >2,150 m LAE (95% CI = 2.8–9.6). Dispersal movements extended to at least 170 km for both sexes ($n = 5$ F, 2 M). At the southern edge of distribution, where suitable and unsuitable conditions exist in close proximity, wolverines selected high-elevation areas near alpine tree-line where a mix of forest, meadow, and boulder fields were present, deep snow-cover existed during winter, and low temperatures near freezing can occur throughout the year. Persistence in these areas where the growing season is brief requires large home ranges that are regularly patrolled, a social system that provides exclusive access to resources, and low densities. These characteristics, along with low reproductive rates, are prevalent throughout the species range, indicating that wolverines are specialists at exploiting a cold, unproductive niche where interspecific competition is limited. The vulnerability inherent in occupying this unproductive niche was likely influential in previous declines within the conterminous United States and will remain a factor as wolverines encounter modern human influences. Conserving wolverines in the conterminous United States will require collaborative management over a large geographic scale. © 2011 The Wildlife Society.

KEY WORDS density, dispersal, *Gulo gulo*, home range, movement, niche, territory, wolverine, Yellowstone.

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Wolverines (*Gulo gulo*) appear to have been extirpated, or very nearly so, from the conterminous United States by about 1930 (Aubry et al. 2007). Although some recovery has occurred (Newby and McDougal 1964, Aubry et al. 2007, Inman et al. 2009, Moriarty et al. 2009) the species is uncommon and has been designated as warranted for protection under the United States Endangered Species Act (U.S. Fish and Wildlife Service 2010). Climate change was considered the primary threat during the listing process (U.S. Fish and Wildlife Service 2010). Other issues of concern include absence from portions of historical distribution (Aubry et al. 2007), potential impacts from increasing levels of backcountry recreational use during winter (Copeland 1996, Greater Yellowstone Coordinating Committee 1999, Krebs et al. 2007), appropriate regulation of human-caused mortality (Krebs et al. 2004), and increasing human infrastructure (Gude et al. 2007). A paucity of data on wolverine ecology in the conterminous United States inhibits the development and implementation of an effective conservation strategy (Ruggiero et al. 2007).

Wolverine ecology has been studied at northern latitudes in taiga, tundra, or boreal montane forests where the predominant ungulate species were moose (*Alces alces*) and caribou (*Rangifer tarandus*; Magoun 1985, Banci 1987, Persson 2003, May 2007). Wolverines in these areas have large spatial requirements, occur at low densities, and have low reproductive rates (Magoun 1985; Whitman et al. 1986; Persson et al. 2006, 2010). However, the conterminous United States sits at the southern periphery of the wolverine's holarctic distribution, and fundamental differences in vegetation, predator, and prey composition, including the possibility of relatively abundant carrion, could result in different spatial use and demographic characteristics.

Wolverine data from the conterminous United States are sparse. According to Ruggiero et al. (2007), the only peer-reviewed journal article reporting wolverine habitat relations, home range size, or behavior through 2007 was a single study in northwest Montana (Hornocker and Hash 1981). Two natal den sites had also been described (Magoun and Copeland 1998), along with dispersal movements of a single male (Inman et al. 2004) and genetic diversity and population structure of wolverines in Montana (Cegelski et al. 2006). More recent publications include works on historical genetics in California (Schwartz et al. 2007), distribution and broadscale habitat relations (Aubry et al. 2007; Schwartz et al. 2007, 2009; Copeland et al. 2010), seasonal habitat associations (Copeland et al. 2007), and fecundity (Anderson and Aune 2008). However, published accounts of even primary metrics such as home range size for adult females remain limited to a single estimate that is somewhat confounded by combining subadult and adult females into 1 average (Hornocker and Hash 1981). Thus, fundamental information on home range size, movement rates, social organization, density, and dispersal is absent or minimal. In addition, telemetry data from within the conterminous United States was obtained in areas that did not contain the full suite of native large carnivores during the period when wolverines were studied, that is, either grizzly bears (*Ursus*

arctos) and/or wolves (*Canis lupus*) were absent (Hornocker and Hash 1981, Copeland 1996). Populations of these large carnivores have continued to expand in recent years (Schwartz et al. 2006, Smith et al. 2010) and may influence wolverine ecology via competition for resources, provisioning of resources (scavenging opportunities), or direct mortality. Our goal was to document and assimilate information on fundamental ecological metrics at the southern edge of distribution to gain a better understanding of the adaptive strategies that enable occupation of the wolverine's niche.

STUDY AREA

Our research occurred at 2 focal areas in the Madison and Teton mountain ranges within the Greater Yellowstone Ecosystem (GYE; Fig. 1). The GYE is 108,000 km² of primarily public lands that include the Yellowstone Plateau and 14 surrounding mountain ranges in Idaho, Montana, and Wyoming (Patten 1991, Noss et al. 2002). Elevations ranged from approximately 1,400–4,200 m. Precipitation increased with elevation and varied from 32 cm to 126 cm of rainfall per year (National Oceanic and Atmospheric Administration 2007, Natural Resources Conservation Service 2007). Snow usually fell as dry powder and depths at higher elevations were often in excess of 350 cm. A variety of vegetative communities were present (Despain 1990). Low-elevation valleys contained short-grass prairie or sagebrush communities. Lower elevation forests included lodgepole pine (*Pinus contorta*) or Douglas-fir (*Pseudotsuga menziesii*), with Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) becoming more common with increasing elevation. Alpine tree-line typically occurred within approximately 150 m of 2,750-m elevation. The highest elevations were alpine tundra or talus fields where snow was typically present for at least 9 months of the year (Natural Resources Conservation Service 2007). Mixed forest types were common throughout the ecosystem and all forest types were interspersed with grass, forb, or shrub meadows. A diverse fauna was present (Bailey 1930, Streubel 1989) and included a variety of ungulates and large carnivores that are not found across much of the wolverine's circumpolar distribution, including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bison (*Bison bison*), pronghorn (*Antilocapra americana*), cougar (*Puma concolor*), bobcat (*Lynx rufus*), badger (*Taxidea taxus*), raccoon (*Procyon lotor*), and coyote (*Canis latrans*). Other species present in GYE and common within wolverine distribution included grizzly bear, black bear (*Ursus americanus*), gray wolf, red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), American marten (*Martes americana*), moose, bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). Public lands and wildlife populations in GYE were managed by 3 State Wildlife Departments (Idaho, Montana, Wyoming), 2 National Parks (Grand Teton, Yellowstone), 6 National Forests (Gallatin, Beaverhead-Deerlodge, Caribou-Targhee, Bridger Teton, Shoshone, Custer), 3 state-level Bureau of Land Management (BLM) offices (Idaho, Montana, Wyoming), 2 National Wildlife Refuges (Red Rocks

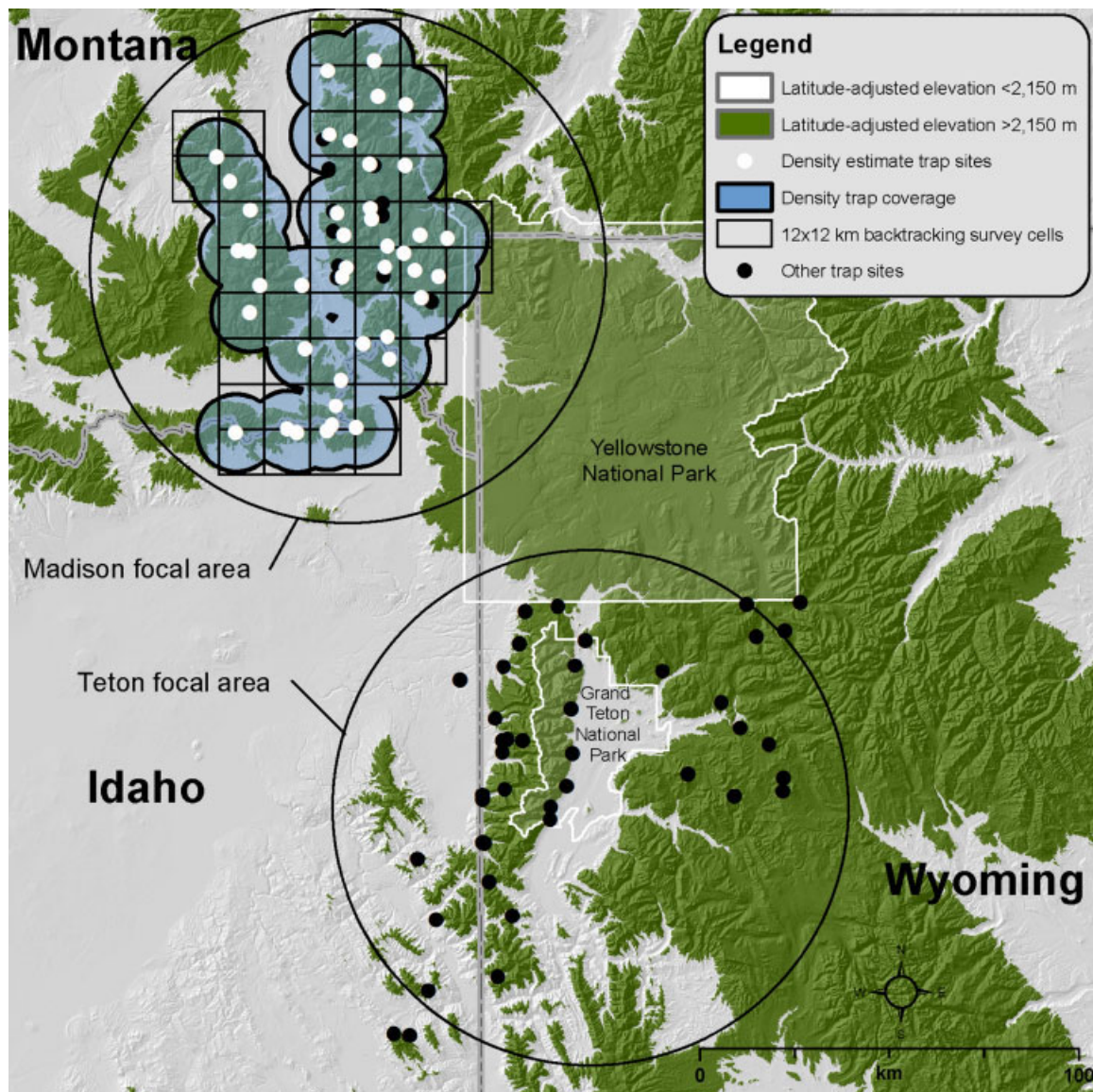


Figure 1. Wolverine study site in the Madison and Teton focal areas, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2001–2008.

Lakes, National Elk Refuge), and additional state and federal entities.

METHODS

Capture, Monitoring, Age-Classification, and Genetic Analysis

We captured wolverines during winters of 2000–2008 using box traps (Copeland et al. 1995, Lofroth et al. 2008) equipped with trap-transmitters (Telonics, TBT-500, Mesa, AZ). We also captured juvenile wolverines by hand at den or rendezvous sites (Persson et al. 2006). We used a variable-powered CO₂ pistol (CO₂ PI, Dan-Inject, Fort Collins, CO) or a hand syringe (juveniles) to deliver an initial dose of approximately 7.5 mg/kg ketamine + 0.25 mg/kg medetomidine (Arnemo and Fahlman 2007). We surgically implanted all wolverines with an intra-peritoneal very high frequency (VHF) radio-transmit-

ter (Advanced Telemetry Systems M1245, M1250, M1255, Isanti, MN; Telonics Imp400L, Imp300L). We administered oxygen at a rate of 0.5 L/min to compensate for the effect of elevation on partial pressure of arterial oxygen (Fahlman et al. 2008, Inman et al. 2009). We followed handling procedures approved by the Animal Care and Use Committees of the Hornocker Wildlife Institute/Wildlife Conservation Society (2000-RMW-504, 2000–2006) and Montana Department of Fish, Wildlife and Parks (IACUC 1–2006, 2006–2007). We attempted to collect aerial VHF telemetry locations at an approximate 10-day interval. We estimated telemetry error by comparing aerial locations with actual ground locations of mortalities, dropped collars, and transmitters placed on the ground. We also fit 12 wolverines with Global Positioning System (GPS) collars programmed to collect locations at various intervals (Televilt POSREC 300, Telemetry Solutions, Concord, CA; Lotek Wireless Inc. 3300SL, Newmarket,

Ontario, Canada). Global Positioning System collars weighed approximately 300 g and we typically programmed the drop-off mechanism to fire after a period of approximately 3 months. We obtained the vast majority of GPS collar data during February and March. We estimated ages based on earliest known alive date, toothwear, cementum annuli, and the lack of descended testes (taken to indicate approximately 12 months of age at winter capture). Based on age of reproductive maturity for female wolverines (Persson et al. 2006), we classified animals ≥ 3 years old as adults and < 3 years as subadults. Subadults referred to as yearlings were 1 to 2 years old, and those referred to as juveniles or cubs were < 1 year old. We collected a small tissue sample from the incision site of each captured wolverine and scat or hair samples from snow-tracked wolverines and dried them in desiccant. All samples were delivered to the United States Forest Service, Rocky Mountain Research Station Genetics Lab, Missoula, Montana for DNA extraction, genotyping, and relatedness analysis as outlined in Inman et al. (2004) and Schwartz et al. (2007).

Habitat Selection, Home Range Size, and Spatial Organization

We conducted a simple first-order habitat analysis (Johnson 1980) using design II (Manly et al. 2002) where we categorized areas into 150-m latitude-adjusted elevation (LAE) bands (Brock and Inman 2006). We developed the LAE layer by using 30-m vegetation data from the National Landcover Dataset (Homer et al. 2001) to regress alpine tree-line within each degree of latitude. We used 2,257 VHF wolverine locations collected from 18 individuals (12 F, 6 M) and the selection ratio function in the R statistical package (Manly et al., 2002, R Core Development Team 2011) to determine which elevation bands were selected for or against by wolverines ($\alpha = 0.05$). We considered November to April to be winter and May to October to be summer.

We used the animal movements extension (Hooge et al. 1999) in Arcview 3.2[®] (Environmental Systems Research Institute, Inc. [ESRI], Redlands, CA) to calculate annual home range size with 2 techniques: 100% minimum convex polygon (MCP; Mohr 1947) and 95% fixed kernel with least squares cross validation (Silverman 1986, Worton 1989). Our annual period for analysis was 1 March to 28 February based on wolverine birth date (Magoun and Copeland 1998). We analyzed data from only those wolverine-years that included > 20 VHF locations over a period of > 225 days. We did not use GPS data to estimate annual home range sizes because of the limited number of individuals fit with GPS collars and short length of time that GPS collars typically collected locations (≤ 3 months). To identify the number and type of political jurisdictions used by each wolverine, we used a Geographic Information System (GIS; ArcGIS 9.2, ESRI) and spatial data delineating the boundaries of federal, state, native American, and private lands (Wyoming Spatial Data Center 1994; Montana Natural Heritage Program 2005; U.S. Bureau of Land Management 2005; U.S. Geological Survey 2005a, b).

We evaluated the degree to which wolverines are territorial with data on movement rates, the time period over which an area $> 75\%$ the size of a multi-year home range was used, and the degree to which home ranges overlapped. We calculated movement distances over independent (separate and exclusive) 2-hr and 24-hr sampling periods with GPS collar data. We related these movement distances to home range size as a means of evaluating whether wolverine home ranges are too large to be defended as a territory (cf. Koehler et al. 1980). We also used GPS locations to assess whether wolverines develop their home range with movements throughout a large proportion of the home range within a few weeks as opposed to seasonal shifts into new areas of the annual range. We accomplished this by calculating the average number of weeks over which resident adult wolverines used an area $> 75\%$ of their multi-year home range size. The first step was construction of multi-year 95% MCP home ranges using all VHF locations of each of 7 resident adults who had been fit with a GPS collar. Then we constructed weekly 100% MCPs using GPS locations, and finally we calculated the proportion of the multi-year home range that was used each week(s). Weeks were cumulative, that is, week 4 included all locations from weeks 1 to 4. To estimate the degree of spatial overlap between individuals, we used data from all pairs of wolverines that had been radio-marked within an individual focal area. Individuals were capable of moving to any point within a focal area, thus each pair had the opportunity to overlap. We did not calculate overlap of a female and her offspring during the offspring's first year. For each pair of wolverines, we calculated a pair of percent area overlaps (PAOs) with annual 100% MCP home ranges constructed with VHF locations. We did this by dividing the total area shared by the individuals during a year by the annual home range of animal A (first PAO) and also by the annual home range of animal B (second PAO; Kernohan et al. 2001). We estimated mean PAO between pairs of wolverines classified by sex (same-sex or opposite-sex) and age-class (adults, adult-subadult, subadults), and tested for differences in PAO between same-sex and opposite-sex pairs within each age-class category using the Wilcoxon rank sum test.

Population Estimation, Density, and Dispersal

We obtained mark-resight data on the Madison focal area during 6 encounter efforts. The Madison focal area was approximately 10,000 km², however we based our estimate of density on a 4,381-km² area as described below. Our first encounter effort (marking) occurred over 3 annual capture periods during winters (Dec–Apr) of 2001–2004. For analysis, we considered only those animals radio-marked and known to be alive on 1 December 2004 to have been captured during the first encounter effort. Our second through fifth encounter efforts consisted of 4 log box capture sessions during winter 2004–2005 (1 Dec–22 Dec, 28 Dec–22 Jan, 23 Jan–17 Feb, 18 Feb–13 Mar). We based trap distribution on the area where wolverines were most likely to occur and the average winter home range size of female wolverines: First, we used 2,150 m LAE as a lower boundary for the area to be effectively covered by our traps. Second, we defined the

area sampled by a trap as a circle, centered on the trap, with an area equivalent to the mean winter home range size for female wolverines (335 km² or 10.33-km radius). We distributed traps so that the aggregate of traps covered >95% of the study area above 2,150 m LAE (Fig. 1). Based on habitat characteristics of successful versus unsuccessful traps during previous years, we placed new traps at or near alpine tree-line as often as possible. Our sixth encounter effort (resight) consisted of a technique that was independent of attracting wolverines to a site. We used snow-tracking to obtain wolverine hair and scat for DNA immediately following the conclusion of the log box capture efforts (Ulizio et al. 2006). We placed a 12 km × 12 km grid over the study area, resulting in 44 cells to be surveyed (Fig. 1). We located the beginning point for a transect above 2,150 m LAE in each cell. Between 21 March and 24 April 2005 we surveyed a 10-km route through wolverine habitat where snow, wind, and terrain conditions were most favorable for encountering tracks and obtaining samples (e.g., wind-blown ridges were avoided). When we encountered a presumed wolverine track, we followed it until obtaining 6 hair samples (a cluster of hair was 1 sample) or 2 scats along each track (Ulizio et al. 2006). We surveyed 10 km within each cell, which did not include distances traveled while following a wolverine track.

We used Program MARK (White and Burnham 1999) to estimate population size using the Huggins (1989, 1991) closed captures model and data from both log box captures and snow-tracking transects. We fit the models M_0 (null), M_t (time), and M_b (behavioral response; Otis et al. 1978), and M_{h2} (2-mixture model for individual heterogeneity; Pledger 2000) to the data, plus an M_t model with occasions constrained equal for the same type of encounter, M_0 with encounter probabilities gender-specific, and M_0 with genotype misidentification errors (Lukacs and Burnham 2005, White 2008). We performed model weighting with second-order Akaike's Information Criterion (AIC_c) weights (Burnham and Anderson 2002) to provide model-averaged estimates. We computed asymmetric confidence intervals based on the log-transformation of the number of animals never encountered added to the number of animals encountered. We used this estimate of population size to derive an estimate of density. As described above, we considered the area sampled for the population estimate to be all areas >2,150 m LAE and within a 10.33-km radius of the traps; thus we sampled a 4,381 km² area (Fig. 1).

We estimated the distance wolverines disperse by determining the distance between the locations of an offspring and the center of the mother's home range. We classified individuals as an offspring when we captured them at a den or rendezvous site with the mother or we established a maternal relationship with a combination of both field observations and genetic data. We considered a dispersal-related movement to have initiated when the offspring was located >2 home range radii from the arithmetic center of their mother's most recent annual 95% fixed kernel home range (Vangen et al. 2001). We considered locations made on separate excursions, that is, to distinct mountain ranges or with a documented return to within 2 home range radii of the center of their

mother's home range, to be independent and indicative of the distances wolverines are capable of dispersing. We measured only the most distant movement for each dispersal-related movement. We estimated age at initiation of dispersal by determining the age of the offspring at the time when they first moved >2 home range radii from the center of their mother's home range.

RESULTS

Between January 2001–February 2008, we captured 30 wolverines (19 F, 11 M). We constructed 92 box traps and captured 29 individuals 107 times during 8,174 trap-nights for an overall trap success rate of 1 wolverine/76 trap-nights. We radio-marked 4 juvenile wolverines at den sites during April–August, and 3 of these were subsequently captured in box traps. We obtained 5,807 relocations (2,359 VHF and 3,448 GPS), and monitored 24 individuals for periods >1 year, 12 individuals for >3 years, and 6 individuals for >5 years through February 2008. We estimated VHF telemetry location error to be 239 m ($n = 17$, SE = 58 m).

Habitat Selection, Home Range Size, and Spatial Organization

We found strong evidence that wolverines were selective in their use of elevation bands annually, during summer, and during winter ($P < 0.001$). On an annual basis, wolverines selected for areas >2,600 m LAE and against areas <2,150 m LAE. During summer, wolverines selected for areas >2,600 m LAE, and during winter selection shifted lower to areas between 2,450 m and 3,050 m LAE (Figs. 2 and 3).

We estimated size of 56 annual home ranges with 2,078 VHF locations of 24 wolverines (15 F, 9 M; Table 1). Minimum convex polygon home ranges of adult females averaged 303 km² whereas adult male home ranges averaged 797 km². Minimum annual home range size for a parturient female was approximately 100–150 km² (smallest during year raising cubs). We located individual wolverines within an average of 4.0 major management units, for example, a National Forest, a National Park, or a BLM district ($n = 25$ wolverines, range = 1–14 management units). We located 80% of these individuals within ≥3 major management units and 52% within ≥4. Eighty-six percent of wolverine locations occurred on lands administered by the United States Forest Service, 12% on National Park Service lands, and 2% occurred on all other ownerships. Thirty-six percent of all wolverine locations occurred in designated wilderness.

We estimated movement rates with GPS collar data for 1,329 independent, straight-line, 2-hr movement distances, and 269 independent, straight-line, 24-hr movement distances. We recorded the vast majority of these movements during winter. Males moved approximately 2–3 times farther than females on average (Table 2). Movement rates of dispersers were similar to resident adults with the exception that dispersers moved a greater maximum distance during a 24-hr period. Based on average 2-hr movement rates, adult wolverines traveled a distance equivalent to the diameter of the

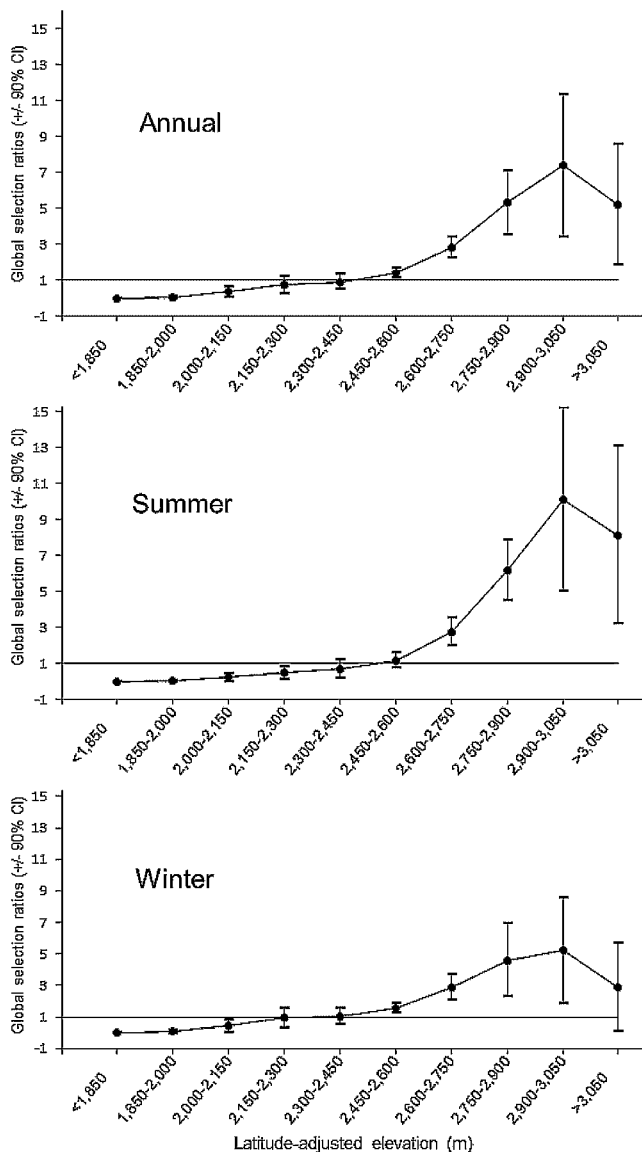


Figure 2. Selection indices (90% CI) for annual and seasonal wolverine use by 150 m latitude-adjusted elevation band, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2001–2008.

average home range in <2 days or around the circumference in <1 week. Travel at maximum observed 2-hr rates would require <6 hr and <24 hr to travel a home range radius or circumference, respectively. Actual minimum distance traveled during a 24-hr interval (multiple GPS locations) averaged 15.5 km for 4 males (range = 0.5–56.6 km, $n = 84$, SE = 1.3 km) and averaged 7.5 km for 6 females (range = 0.0–27.9 km, $n = 185$, SE = 0.39 km).

We estimated temporal development of annual home ranges for 7 resident adult wolverines that were monitored for 2–6 years with VHF transmitters and also fit with a GPS collar (5 F, 2 M, \bar{x} years monitored with VHF = 4, \bar{x} GPS locations = 390). These wolverines used an area $\geq 75\%$ of their multi-year MCP home range size in an average of 4.6 weeks (32 days; range = 1–7 weeks; Fig. 4). A recently parturient female required the maximum number of weeks to use an area $\geq 75\%$ of her multi-year

home range. When we omitted this individual, the wolverines used 87% of their multi-year home ranges in an average of 29 days. Thus, extensive movements throughout the annual home range occurred over brief time intervals for both sexes. The above movements occurred during winter; however, VHF data indicated that similar movements likely occur during other seasons.

Overlap of home ranges between adult wolverines of the same sex was minimal and the shared area was <2% of either home range in all but 1 case (Table 3). In 2 cases, extensive GPS data did not reveal any significant forays into an adjacent same-sex territory, rather it confirmed the lack thereof (Fig. 5). Degree of overlap was greater for opposite-sex pairs than for same-sex pairs of adults ($Z = 4.04$, $P < 0.001$) and subadults ($Z = 2.09$, $P = 0.04$). Overlap did not differ between same-sex or opposite-sex adult-subadult pairs ($Z = -1.57$, $P = 0.12$). On each of the 4 occasions when a resident adult wolverine died, same-sex adults that we had not previously located within the dead individual's home range began using portions of the unoccupied home range, or same-sex subadults expanded into the dead individual's former home range and occupied most or all of it (Fig. 6). Movements into these dead adults' former home ranges occurred within a maximum of 3–7 weeks. We also captured a same-sex yearling in the former home range of a dead subadult on 3 occasions. These captures occurred late in our capture effort (after 63–90 days of multiple traps operating in the areas the wolverines subsequently used) and captured individuals were 11.5–12.5 months of age, suggesting that they may have recently dispersed into the vacated areas.

Population Estimation, Density, and Dispersal

Five radio-marked wolverines were alive and in the study area at the initiation of our recapture efforts during December 2004. We monitored 15–24 log box traps between 5 December 2004 and 13 March 2005 (1,980 trap-nights), and we captured 10 wolverines 19 times (second through fifth encounter efforts). During the sixth encounter effort (snow-tracking) we sampled each of the 44 12 km \times 12 km grid cells with a 10-km transect. We were not able to accomplish a second round of 10-km transects because of unusually high avalanche danger and poor tracking conditions that spring. Three of 6 tracks confirmed as wolverine via DNA provided DNA of high enough quality to obtain an individual identification; 2 were marked wolverines, and 1 was unmarked. Overall, we recaptured 4 of 5 wolverines marked during the first encounter effort (those marked during previous winters and alive at initiation of the density estimate) and identified 7 new individuals. The model weighted average population estimate was 15.2 wolverines (95% CI = 12.3–42.0) with individual model estimates ranging from 13.9 to 18.2 wolverines (Table 4). We based our estimate of density on 4,381 km² of area >2,150 m LAE that was sampled by our trap distribution. This yielded a density estimate of 3.5 wolverines/1,000 km² of area >2,150 m LAE (95% CI = 2.8–9.6). This estimate did not include any cubs of the year (born Feb–Mar 2005).

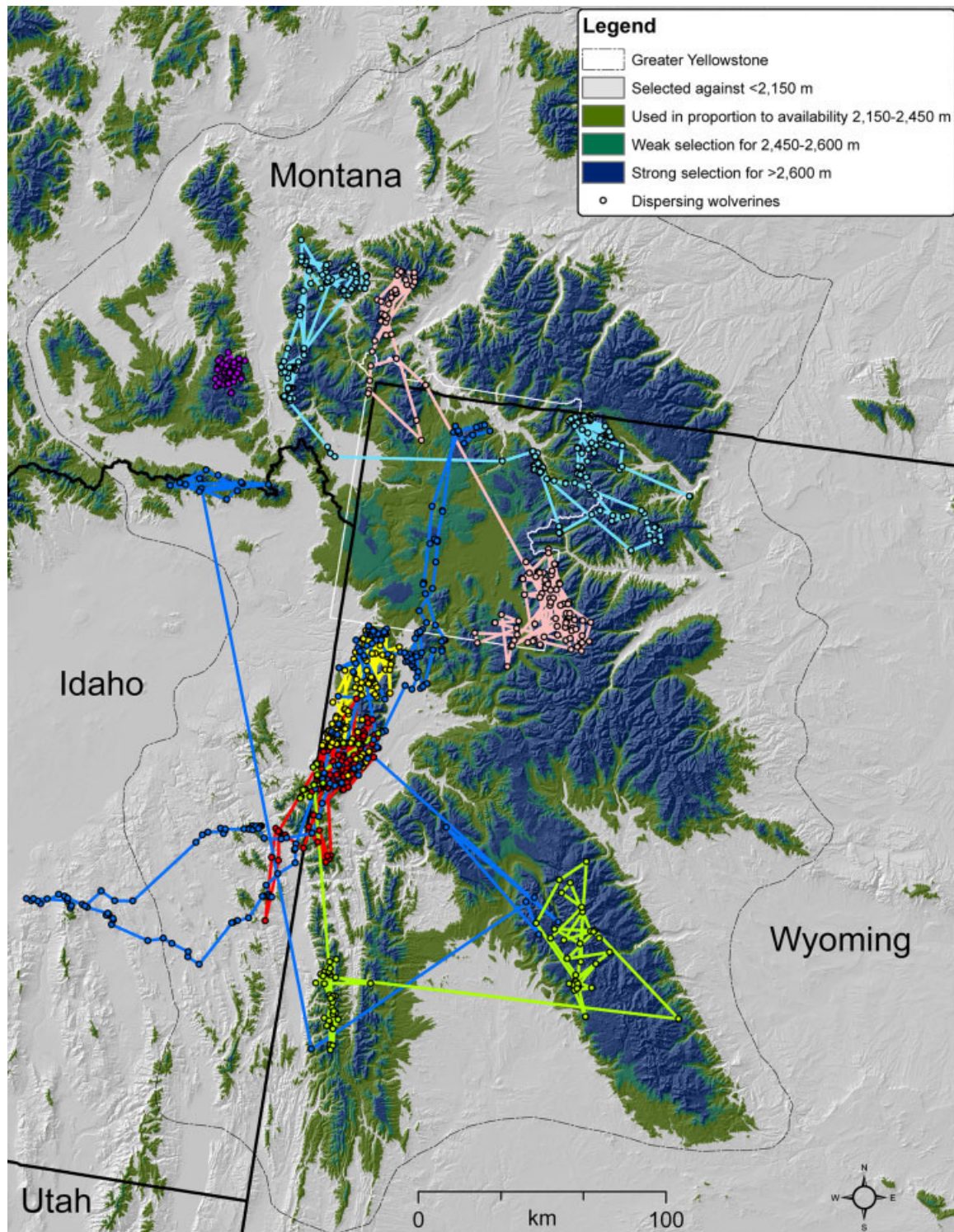


Figure 3. Annual wolverine habitat selection by 150 m latitude-adjusted elevation band, and wolverine dispersal movements, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2001–2008. Each color represents a different individual and consecutive locations are connected with a straight line. Males are blues and all other colors are females.

We documented 25 dispersal-related movements made by 7 offspring (5 F, 2 M; Fig. 3). Maximum distance from the mother's home range center was 170 km for males and 173 km for females. Average maximum distance per dispersal-related movement was 102 km for males ($n = 10$, $SE = 16.4$ km) and 57 km for females ($n = 15$,

$SE = 13.5$ km). First documented dispersal-related movements occurred at 11.4 months of age on average (range = 8.4–14.1 months, $n = 6$). Pulses of dispersal-related movements occurred near the time when litters are born and snow conditions may facilitate travel (Fig. 7).

Table 1. Mean annual (1 Mar–28 Feb) home range size (km²) of radio-marked wolverines using 95% fixed kernel (FK) and 100% minimum convex polygon (MCP) estimators, Greater Yellowstone Ecosystem of Idaho, Montana and Wyoming, USA, 2001–2007^a.

Sex	Age-class	w^b	n^c	I^d	Days ^e	95% FK		100% MCP	
						Mean	SE	Mean	SE
Female	Adult	8	20	41	357	400	92	303	54
	Subadult	10	17	35	343	1,175	383	884	297
Male	Adult	5	13	36	346	1,160	155	797	87
	Subadult	6	6	32	341	3,292	1,527	2,689	1,565

^a Very high frequency (VHF) locations only; all individuals were located >20 times over a minimum 225 day period.

^b Number of individual wolverines; annual home ranges of 3 females and 2 males were measured as both subadults and adults.

^c Number of annual home ranges.

^d Mean number of locations per annual home range.

^e Mean number of days monitored during annual home range.

Table 2. Wolverine movement distances (km) during 2-hr and 24-hr periods as determined with Global Positioning System (GPS) collars, Greater Yellowstone Ecosystem of Idaho, Montana and Wyoming, USA, 2002–2007.

Sex	2-hr Movement distances (km)					24-hr Movement distances (km)				
	w^a	n^b	Mean	Range	SE	w^a	n^b	Mean	Range	SE
Female	7	785	0.90	0.00–7.67	0.05	6	185	4.59	0.00–17.45	0.30
Male	5	544	1.90	0.00–13.82	0.10	4	84	12.04	0.02–54.01	1.13

^a Number of individual wolverines.

^b Number of independent (non-overlapping), straight-line movements.

DISCUSSION

Wolverines in GYE selected elevations at and above tree-line during summer and shifted to slightly lower areas centered at tree-line during winter. This pattern was similar to wolverines in northwest Montana and Idaho (Hornocker and Hash 1981, Copeland et al. 2007). Although wolverines shifted lower during winter, they still avoided the low-elevation winter ranges where there were thousands of elk, scavenging opportunities, and virtually no human activity. The nearly complete lack of tree or talus escape cover at low elevations along with the presence of potential predators (wolves and cougars) and competitors (coyotes, bobcats, wolves, and cougars) may have discouraged wolverine use of these areas. Habitat in the areas wolverines selected was characterized by steep terrain with a mix of tree cover, alpine meadow, boulders, and avalanche chutes. Deep snow exists during winter, and the wolverine's large feet allow it to travel relatively easily in these environments. Temperatures in these areas are generally cool and can fall below freezing during any month. Snow persists in patches well into summer. As a result, the growing season in the areas wolverines inhabit in GYE are brief and relatively unproductive. The correlation between wolverine presence and persistent spring snow cover (Copeland et al. 2010) suggests that occupying cold, snow-covered, and relatively unproductive environments is a common pattern throughout the global distribution of the species. For wolverines, an apparent tradeoff exists between resource acquisition on one hand and avoidance of predation and competition on the other. Wolverine balance these competing interests by exploiting an unproductive

niche where predation and interspecific competition are reduced.

Home range size of GYE wolverines was large relative to body size. Comparison of minimum reported home range size of female carnivores typically weighing 6–12 kg in North America indicates that wolverine home ranges are 21–104 times larger than those of the coyote, badger, and bobcat, 8 times that of lynx, and over 500 times that of the raccoon (Anderson and Lovallo 2003, Bekoff and Gese 2003, Copeland and Whitman 2003, Gehrt 2003, Lindzey 2003). Despite differences in habitat, competitor, predator, and prey composition, the wolverine home range sizes we measured were similar to those reported elsewhere in the conterminous United States and British Columbia (Hornocker and Hash 1981, Copeland 1996, Krebs et al. 2007). Home range size of mammals is related to body mass, and within a trophic class a species living in less productive habitat will have a larger home range than that predicted by the generalized relationship between home range and body mass (Harestad and Bunnell 1979). The home range size of wolverines indicates that their niche is based upon exploitation of relatively unproductive habitats. The smaller home ranges reported from wolverine studies at more northern latitudes (Magoun 1985, Persson et al. 2010) suggest either that resources are more limited in GYE or that competition for resources is more intense.

Spatial distribution patterns of the Mustelidae are typically described as intra-sexual territoriality, where only home ranges of opposite sexes overlap (Powell 1979). Wolverine-specific reports exist for both intra-sexual territoriality (Magoun 1985, Copeland 1996, Hedmark et al.

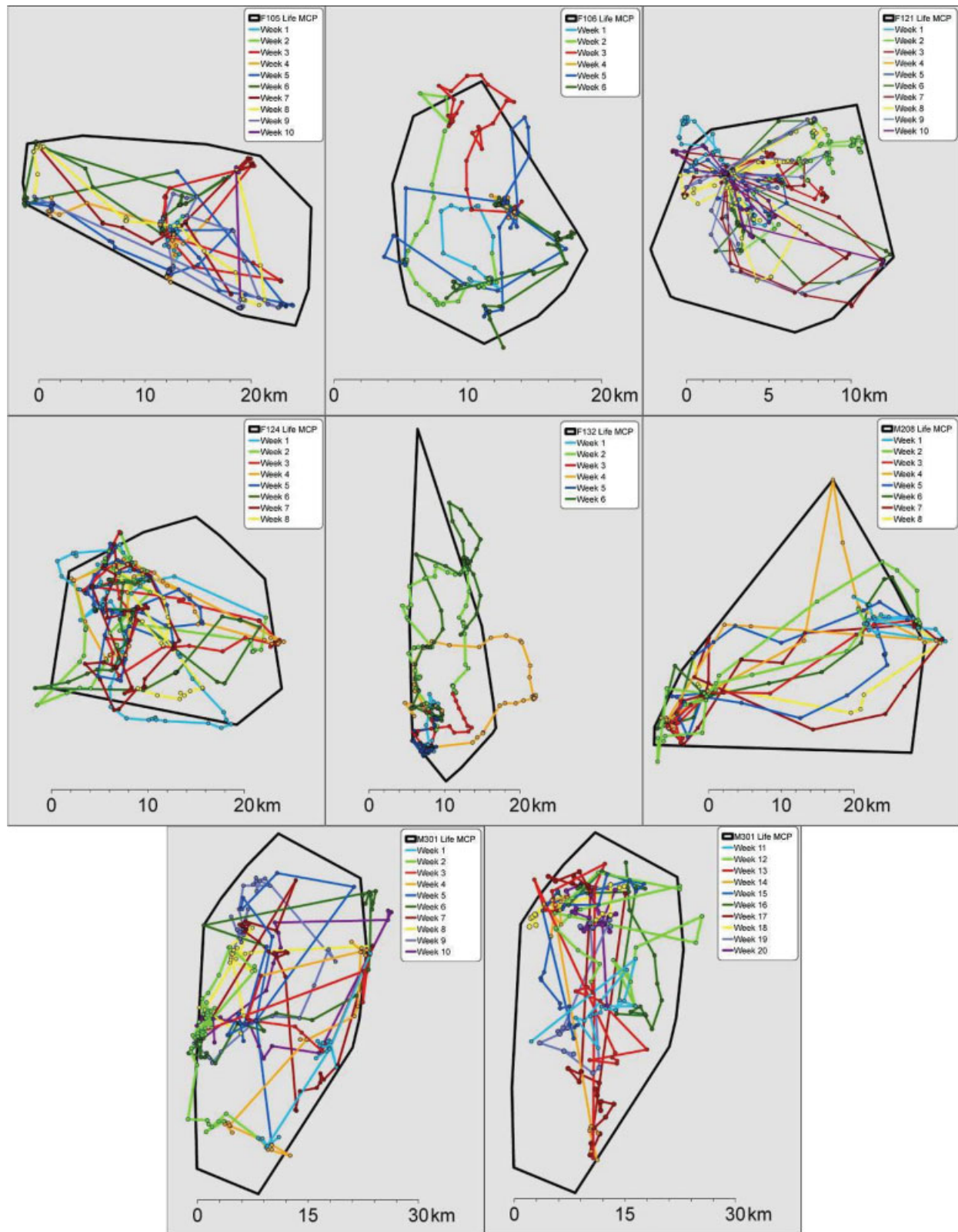


Figure 4. Weekly movements of resident adult wolverines (5 F, 2 M) recorded with Global Positioning System collars, Greater Yellowstone Ecosystem of Idaho, Montana and Wyoming, USA, 2004–2007. Black polygons are multi-year 95% minimum convex polygon (MCP) home ranges and each color represents movements during a 1-week period.

Table 3. Mean percent area overlap of annual 100% minimum convex polygon home ranges by same-sex and opposite-sex pairs of adult, adult–subadult, and subadult wolverines, Greater Yellowstone Ecosystem of Idaho, Montana and Wyoming, USA, 2001–2006^a.

Sex-age class category	<i>n</i> (pairs)	Percent area overlap			
		Mean	SE	95% CI	<i>P</i> -value
Adult pairs					
Same-sex	22	2.1	1.6	0.0–5.3	<0.001
Opposite-sex	17	25.9	6.1	13.8–37.9	
Adult–subadult pairs					
Same-sex	34	12.7	2.7	7.4–18.0	0.12
Opposite-sex	34	24.1	4.3	15.8–32.5	
Subadult pairs					
Same-sex	11	5.4	3.4	0.0–12.1	0.04
Opposite-sex	10	21.4	7.7	6.3–36.4	

^a Very high frequency (VHF) radio-locations only; annual home range is 1 March–28 February.

2007, Persson et al. 2010) and for a high degree of spatial overlap but with temporal separation (Hornocker et al. 1983). Arguments against territoriality by wolverines include the lack of ability to defend such a large home range (Koehler et al. 1980). Our data on movement rates in relation to home range size, temporal development of the home range, minimal overlap of same-sex adults, and relatively immediate shifts upon a death suggest that wolverines are capable of patrolling a large territory and provide further support for intra-sexual territoriality. Reproductive success is closely correlated to the amount of energy that a female wolverine can obtain (Persson 2005), and for predators that are capable of individually acquiring prey, the presence of conspecifics reduces foraging efficiency (Sandell 1989). Since wolverines feed on individually obtainable prey and occupy relatively

unproductive habitats, it follows that behaviors for maintaining exclusive access to resources would likely have selective advantage. Frequent marking behavior (Pulliainen and Ovaskainen 1975, Koehler et al. 1980) is likely part of an adaptive strategy that involves maintenance of exclusive territories within sexes so that feeding and breeding opportunities are monopolized by dominant individuals and their immediate offspring.

Although comparisons of density among wolverine studies must be made with caution because of the variety of methods used and wide confidence intervals (Table 5), our estimate of 3.5 wolverines/1,000 km² is at the low end of reported values for North America and low relative to other carnivores in GYE. For example, pre-1990 density estimates for the threatened Yellowstone grizzly bear (near low point) were in the range of 9–12 bears/1,000 km² (Schwartz et al. 2006), approximately triple that of our estimate for wolverines. Applying our wolverine density estimate across the entire 52,375 km² area of the GYE that lies above 2,150 m LAE (Fig. 3) suggests the potential for 182 wolverines. However, the current population size is likely much smaller since much of this area is not proximate to landscapes at elevations that were strongly selected (e.g., the interior of Yellowstone National Park; Fig. 3), and every wolverine we monitored used elevations that were strongly selected. Furthermore, large areas of GYE recently surveyed for wolverines did not result in detections (Murphy et al. 2011), and presence/density in other large areas of GYE such as the Wind River Range is unknown. In any case, wolverine density at present, and likely historically, is low and therefore the population is small and relatively vulnerable. This vulnerability likely contributed to historic wolverine population declines in the conterminous United States that occurred earlier than declines of other carnivores that were specifically persecuted (Paquet and Carbyn 2003, Schwartz et al. 2003, Aubry et al. 2007).

The dispersal distances we measured in GYE indicate that wolverine populations occur over a vast geographic area where management decisions are made by a diversity of jurisdictional authorities. Vangen et al. (2001) reported maximum dispersal distances of 101 km for 11 male and 178 km for 11 female wolverines in Scandinavia. However, they

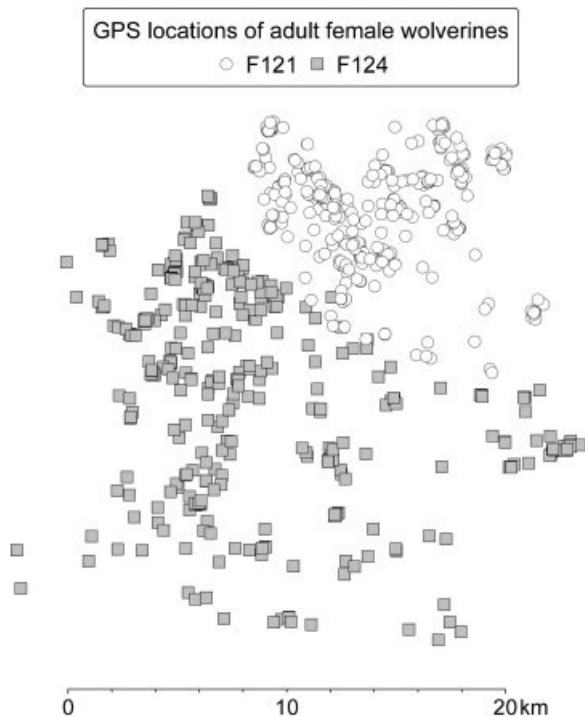


Figure 5. Global Positioning System (GPS) locations of 2 adult female wolverines with adjacent home ranges, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, February–April 2007.

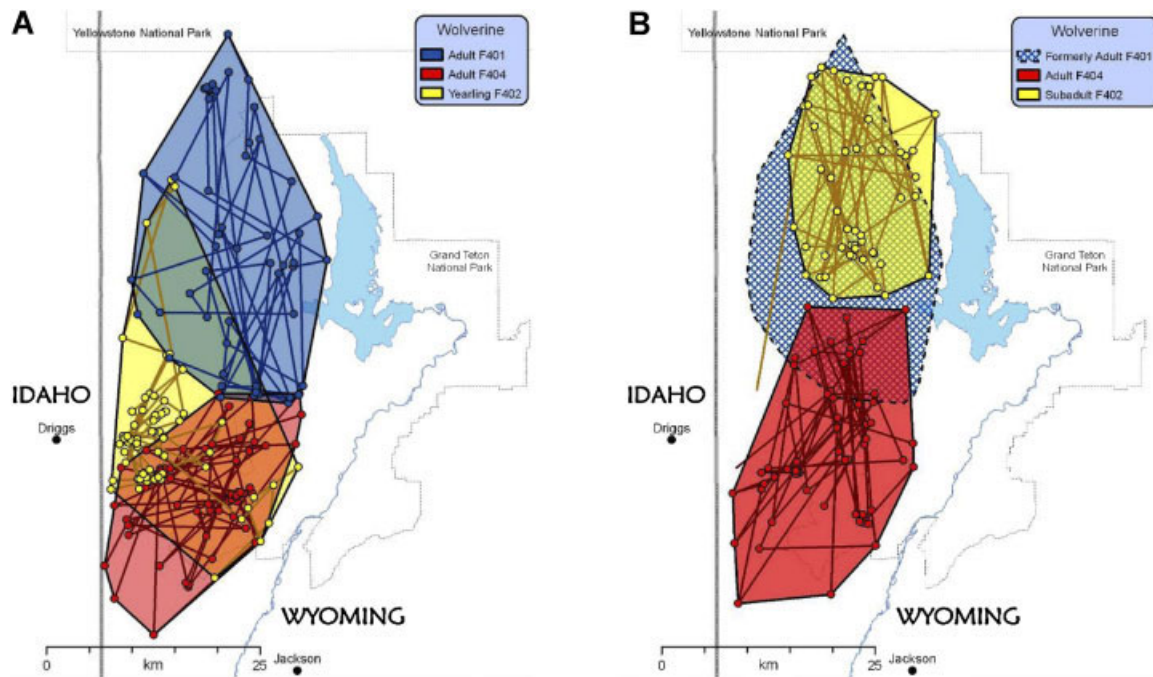


Figure 6. Female wolverine locations, movements, and annual 100% minimum convex polygon (MCP) home ranges (A) before and (B) after the death of adult female F401, Teton Range, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2002–2004.

cautioned that this might be an underestimation. Our data indicate that both males and females are capable of dispersing to areas at least 170 km from their mother's home range; however, this may also underestimate the distances wolverines disperse. For example, using a GPS collar, we documented an exploratory movement by a male that extended 112 km from its mother's center of activity and covered over 200 km in less than 6 days. Therefore, single instances when wolverines are unable to be located during weekly telemetry flights may be the result of a long-distance movement. Despite regular aerial searches including extensions over large portions of GYE, M304 was missing for periods of 334, 189, and 136 days, and F421 for 82 days (Fig. 7). We believe it likely that these individuals moved beyond the GYE. Duration of monitoring may also be a factor in under-

estimating dispersal distances. Of the 4 offspring we documented dispersing long distances (>150 km), all initiated significant movements at 11–13 months of age, and 2 of these 4 individuals made additional long distance movements (>145 km) at 23–24 months of age (Fig. 7). One individual moved >225 km between 36 months and 40 months of age. Wolverines estimated to be 2 to 3 years old made several movements of approximately 200 km in Idaho (Copeland 1996). Therefore, wolverine dispersal can occur over multiple years and monitoring individuals for several years might be required to fully understand dispersal patterns. Wolverines have traveled as far as 300 km and 378 km in Alaska (Magoun 1985, Gardner et al. 1986), and genetic sampling suggests the potential for wolverines to disperse as much as 500 km (Flagstad et al. 2004).

Table 4. Estimated population size and density of wolverines in the Madison, Gravelly, and Centennial Mountain Ranges of the Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, December 2004–April 2005.

Model ^a	Model weight	Population estimate	SE	95% CI	Density (95% CI) (wolverines/1,000 km ²) ^b
M_0	0.32	14.1	2.04	10.1–18.1	3.2 (2.3–4.1)
M_0 + gender	0.32	15.6	3.87	8.0–23.1	3.6 (1.8–5.3)
M_b	0.16	18.2	10.78	0.0–39.3	4.2 (0.0–9.0)
M_0 + genotype	0.11	14.1	2.04	10.1–18.1	3.2 (2.3–4.1)
M_t with occasions equal	0.05	14.1	2.03	10.1–18.0	3.2 (2.3–4.1)
M_{h2}	0.04	14.1	2.04	10.1–18.1	3.2 (2.3–4.1)
M_t	0.01	13.9	1.92	10.1–17.7	3.2 (2.3–4.0)
Weighted average		15.2	5.24 ^c	12.3–42.0 ^d	3.5 (2.8–9.6)

^a M_0 = null model; M_0 + gender = encounter probabilities gender specific; M_b = behavioral response; M_0 + genotype = genotype misidentification errors; M_t with occasions equal = occasions constrained equal for encounter type; M_{h2} = 2-mixture model for individual heterogeneity; M_t = time.

^b Area sampled was 4,381 km² above 2,150 m latitude-adjusted elevation.

^c Unconditional SE.

^d Based on calculation of asymmetric confidence interval using unconditional SE.

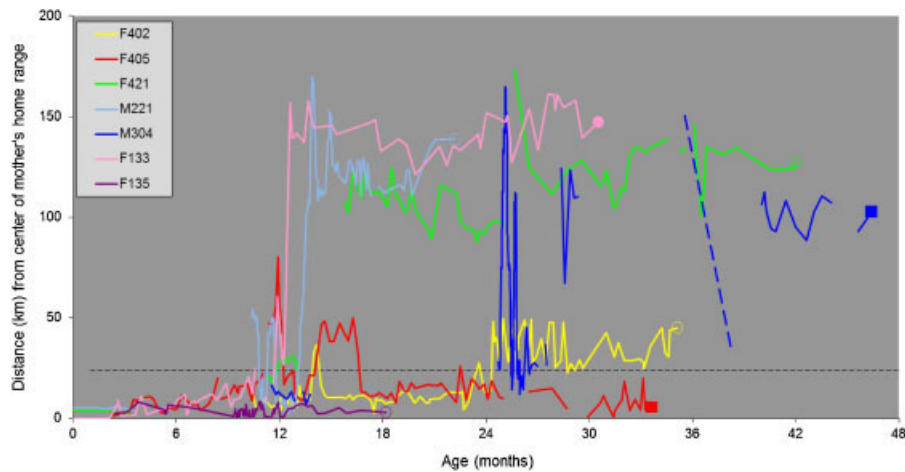


Figure 7. Distance, age at initiation, and duration of dispersal related movements of 7 wolverines (5 F, 2 M), Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2001–2007. The black dashed line represents the diameter of the average adult female home range. Gaps in lines representing wolverines indicate periods where the individual was searched for but could not be located. Filled circles represent individuals that were still being monitored as of 28 February 2008; open circles represent individuals that were missing or whose transmitter has failed; a square represents a dead individual. The blue dashed line indicates an undocumented but likely move by M304 through or near the mother's home range between known locations in distant mountain ranges.

Table 5. Wolverine density estimates (wolverines/1,000 km²) from North America.

Density	95% CI	Location	Refs.	Method
15.4		Montana	Hornocker and Hash (1981)	Census, home range
14.1 ^a		Alaska	Magoun (1985)	Census, home range
9.7	8.5–10.9	Yukon	Golden et al. (2007)	Quadrat sampling
9.7	5.9–14.9	Alaska	Royle et al. (2011)	Camera-trapping
6.5	2.8–10.2	N British Columbia	Lofroth and Krebs (2007)	Mark-recapture-resight
5.8	3.6–7.9	S British Columbia	Lofroth and Krebs (2007)	Mark-recapture-resight
5.6		Yukon	Banci and Harestad (1990)	Census, home range
5.2	3.1–7.2	Alaska	Becker (1991)	Transect intercept probability
4.5		Idaho	Copeland (1996)	Census, home range, reproduction
3.5	2.8–9.6	Yellowstone	This study	Mark-recapture-resight
3.0	2.2–3.8	Alaska	Golden et al. (2007)	Quadrat sampling

^a Estimate occurred during autumn so included cubs of the year.

By synthesizing information on spatial ecology at the edge of distribution, where both suitable and unsuitable conditions exist in close proximity, clear patterns emerge and help clarify the wolverine's niche. In the presence of a diverse assemblage of ungulates and carnivores at the southern periphery of their distribution, wolverines select high elevation habitats where deep snow exists during winter, the growing season is brief, and food resources are relatively limited. Although most large carnivores (e.g., bears, wolves, and cougars) either hibernate or migrate along with elk and deer herds during winter, the wolverine remains active at higher elevations, using its large feet to patrol a vast, frozen territory that is covered in snow. Successful exploitation of these unproductive environments requires large home ranges that are regularly traversed, territories that provide exclusive intra-specific access to resources, and low densities. These characteristics, along with low reproductive rates, are prevalent throughout the species range (Magoun 1985; Landa et al. 1998; Persson et al. 2006, 2010; Golden et al. 2007). When viewed together, these characteristics indicate that wolverines are specifically adapted to exploit a cold, unpro-

ductive niche where resources are scarce and interspecific competition is limited. Success within this niche likely requires behavioral adaptations that make efficient use of the limited food resources, including strategies for outcompeting other scavenging organisms such as insects and bacteria. Research on the specific mechanisms wolverines use to occupy their cold, snowy niche could improve conservation strategies, including those related to climate change.

MANAGEMENT IMPLICATIONS

The once-extirpated wolverine population of the conterminous United States has responded positively to the regulation of intentional human-caused mortality that was the major thrust of wildlife conservation during the 20th century. However, because of the unproductive niche wolverines have evolved to occupy, this species will be vulnerable again, this time to the conservation challenges of the 21st century, such as roads, rural sprawl, recreation, and climate change (Gude et al. 2007, Krebs et al. 2007, Packila et al. 2007, Copeland et al. 2010). Clearly, the wolverine population of GYE is cumulatively influenced by a complexity of land

ownerships and management authorities. Therefore, similar to grizzly bear management (Interagency Conservation Strategy Team 2007), implementation of a conservation strategy that addresses wolverine needs in a coordinated fashion is more likely to ensure persistence. However, in the case of the wolverine, this GYE scale is likely too small for a viable population. A viable population may require an area as broad as the western United States and, as such, wolverine management in GYE and other areas would be most effectively designed by considering each area's role within the context of the larger metapopulation. Designing effective metapopulation conservation strategies would be greatly facilitated by development of an empirical prediction of wolverine habitat across the western United States, particularly one distinguishing among areas suitable for use by resident animals, reproductive females, and dispersal movements. With this tool it would be possible for multiple management entities to conceptualize and collaboratively implement practices facilitating survival, reproduction, and gene-flow at the most effective locations from the metapopulation perspective.

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